

Quantifying aspects of the evolution of endothermy

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ABSTRACT

Various conceptual or qualitative models have been proposed to explain the evolution of homeothermic endothermy from heterothermic ectothermy. Assessment of the feasibility of these models may benefit from quantitative analyses of hypotheses deriving from them. In this study, a quantitative approach was applied to a recent conceptual model which proposed a stepwise progression from ectothermy to endothermy in a medium sized vertebrate “evolving” in a warm, mesic thermal environment. By assuming that selection acted to maximise time available for activity, this study showed that endogenous heat, whether from activity or shivering thermogenesis, increased time within nominal preferred body temperatures only if low values of thermal conductance associated with insulation were already in place. Further, this study demonstrated that benefits were enhanced if the insulation was by-passable and associated with a wide range of thermal conductance. Because aerobic scope was incorporated as a constraint to thermogenic capacity, increases in standard metabolic rate were relatively ineffective until they were substantial and, at one stage, plesiomorphic daily torpor emerged, at least in the circumstances modelled. Also emerging from the modelling were the thermal neutral zone and basal metabolic rate characteristic of homeothermic endotherms. Additionally, benefits from rudimentary turbinal scrolls were quantified for this modelled, hypothetical animal in this particular environment. This initial exploratory study demonstrated how quantifying aspects of proposed models for the evolution of endothermy can provide insight into their feasibility. In so doing, this quantitative modelling highlighted avenues for further enquiry and demonstrated one tool for addressing debate about the evolution of endothermy.

Key words: modelling, endothermy, ectothermy, evolution, thermal conductance, metabolic rate

Introduction

Endothermy has apparently evolved independently in a number of vertebrate clades; most prominently, at least amongst current vertebrates, in birds and mammals. Not surprisingly, endothermy has excited biologists and a number of models have been proposed to explain its evolution (e.g. Crompton, *et al.* 1978; McNab 1978; Bennett 1991). Most such models are conceptual or qualitative. It would be instructive to investigate, and eventually compare, models in a quantitative way, perhaps evaluating advantages accruing to endotherms that evolved in the various ways proposed.

In a series of recent papers, Grigg and Beard (2000), Grigg (2004) and Grigg *et al.* (2004) proposed a stepwise progression from an ectothermic therapsid towards a variety of endothermic mammals, both heterothermic and homeothermic. Salient features of this progression included, but were not limited to:

- i) that by-passable insulation evolved first and is a prerequisite for effective maintenance of a high and stable body temperature,
- ii) that even before the evolution of mammalian metabolic rates, the heat generated by activity or perhaps by shivering thermogenesis, if retained, may have advantages for temperature dependent physiological processes and

iii) that heterothermy (torpor and hibernation) is plesiomorphic among endotherms, a remnant of ectotherm heterothermy that was retained (or re-expressed) in many mammals, refined in those that needed to survive periodically harsh environments and abandoned in those where energetic resources were sufficient and reliable.

To develop their model, Grigg *et al.* (2004) compared the thermoregulation of extant reptiles and mammals. Based in part on data from brooding pythons and from heterothermic echidnas, they concluded that reptiles and mammals share many thermoregulatory attributes and that the differences between the classes are more quantitative than qualitative.

In this, an initial study, quantitative modelling was used to convert an ectotherm with lizard physiology into something approaching an endotherm with mammalian physiology using the step-wise progression of Grigg *et al.* (2004) as an approximate guide. Specifically, a heat budget model was used to predict the body temperature of a medium sized, hypothetical animal living in a warm, mesic environment as it progressed through various stages in this evolution. Time spent within specified preferred body temperature ranges was used to evaluate advantages accruing to the animal at various stages of the evolution in such a way as to test the three salient features listed above as hypotheses deriving from the model of Grigg *et al.* (2004).

Methods

Quantitative Modelling

The modelling used and its verification are described in more detail elsewhere (Brice 2008). Briefly, the modelling solves commonly used heat budget equations for body temperature (T_b) of any medium sized animal in either static or dynamic thermal environments. It accomplishes this by solving the cooling/heating curve equation:

$$T_{b,t} = T_{b,eq,t} - (T_{b,eq,t} - T_{b,t-1})e^{-\delta t/\tau} \quad \text{Eq. 1}$$

for T_b at time t ($T_{b,t}$) given that the thermal time constant, $\tau = C/K_{o,eq,t}$ where C is the overall heat capacity of the animal's tissues and $K_{o,eq,t}$ is the overall thermal conductance of the animal in equilibrium at time t . In this study $\delta t = 10$ minutes. In equation 1, $T_{b,eq,t}$ is the equilibrium body temperature at time t which is calculated for each t ($= 10, 20, 30 \dots$ min) by solving:

$$M_{eq,t} = K_{o,eq,t} (T_{b,eq,t} - T_{e,eq,t}) + E_{eq,t} \quad \text{Eq. 2}$$

and

$$M_{eq,t} = M_{eq,0} Q_{10}^{\frac{(T_{b,eq,t} - T_{b,eq,0})}{10}} \quad \text{Eq. 3}$$

simultaneously for $T_{b,eq,t}$ and $M_{eq,t}$: the metabolic heat production (M) of the animal when in equilibrium at time t . In equation 2, $E_{eq,t}$ is the evaporative heat lost for the animal when in equilibrium for a given $K_{o,eq,t}$ and $T_{e,eq,t}$. $T_{e,eq,t}$ in this study was $T_{e,t}$, the operative temperature at time t and was the driving variable for the simulations. $K_{o,eq,t}$ here was generally determined so as to maximise time spent within a range of preferred T_b (T_{pref}). That is, K_o was varied automatically within the simulations. In the absence of sweating, evaporative cooling in general (E) can be determined from respiratory evaporative heat loss alone as:

$$E = \lambda_{T_b} V_i (\chi_{(T_b - T_{ue})} - h_{Ta} \chi_{Ta}) \quad \text{Eq. 4}$$

where λ_{T_b} is the latent heat of evaporation at T_b , V_i is the respiratory minute volume (in $\text{ml} \cdot \text{min}^{-1}$) which may be varied with M (see below), χ_{T_b} is the absolute humidity of air saturated at temperature T_b , h_{Ta} is the relative humidity measured at T_a and T_{ue} is the effect any turbinal scrolls may have on the temperature of the expired air. For equation 2, $E_{eq,t}$ may be determined by substituting $T_{b,eq,t}$ and similarly appropriate values for V_i , T_{ue} etc. into equation 4. In equation 3, $M_{eq,0}$ and $T_{b,eq,0}$ are the initial M and T_b for the simulation, but only if they are in equilibrium with T_e and other parameters at the start. If not, as in many of the simulations in this study, other equilibrium values for a given T_e may be used as substitutes. A convenient choice used here was the SMR that pertained (according to the simulations, below) for a given T_b in equilibrium with a given T_e .

In summary, the modelling proceeds from a defined starting point by determining $T_{b,eq,t}$ for each t and then calculating the approach of T_b to $T_{b,eq,t}$ over each ten minute interval. Note that the system may never reach equilibrium at any stage because equilibria are constantly

recalculated. The resultant time course of $T_{b,t}$ reflects the cooling or heating of the animal in response to ever changing equilibria which in these cases were determined primarily by fluctuations in operative temperature (see below). In this way, environmental dynamics can be incorporated into the modelling. This modelling was found to predict well the time course of T_b in various animals including lizards and mammals in static and dynamic thermal environments (Brice 2008).

Assumptions and Constraints

It was assumed that important physiological processes proceed optimally at particular T_b , and further, that if a capacity for more precise thermoregulation evolved, natural selection acted to increase the efficiency of physiological processes over ever more narrow ranges of T_b . Thus, a range of preferred body temperatures (T_{pref}) was defined for the various simulations. Initially, this specified range was wide (25°C to 35°C) but feasible when compared to some extant lizards (Heatwole 1976) and allowed the virtual lizard more than a trivial part of the day for activity etc. Subsequently, T_{pref} was narrowed to reflect more typical mammalian physiology as evolution progressed. The amount of time spent within T_{pref} was used as a response variable, reflecting the assumption that increasing time spent at these T_b had advantages for activity, foraging, digestion, reproduction and so on.

In accordance with the step-wise progression proposed by Grigg *et al.* (2004), metabolic heat, both from activity and from (shivering) thermogenesis, were added at an early stage. To retain some realism, these thermogenic capacities were constrained to being no more than about 10 times the standard metabolic rate (SMR) for a T_b of 25°C , and this aerobic scope was retained throughout all the stages of the simulated evolution.

Respiratory minute volume was set initially to be typical for a lizard. Assuming a constant oxygen extraction efficiency for all simulations, V_i was varied in direct proportion to M both within and between simulations. Thus, as the evolution progressed, this modelling took no account of the evolution of the anatomy of the mammalian lung, except for a straight forward increase in capacity to aspirate increasing metabolic rates. Similarly, turbinal scrolls, commonly associated with the saving of heat and/or moisture in endotherms (Hillenius and Ruben 2004), were assumed to be absent in the initial virtual lizard. For the sake of simplicity, they were omitted until after an endotherm-like animal had been derived by the modelling, at which time they were included. In this way, the benefit of having turbinal scrolls, even though the environment was warm and mesic, was quantified for an endotherm.

Sweating was assumed to be absent in the initial virtual lizard and in all subsequent simulations. Therefore, all evaporative water loss was assumed to be respiratory. Additionally for simplicity, any panting response to high body temperatures was omitted throughout. Thus none of the cooling mechanisms displayed by either reptiles or mammals, other than changes in thermal conductance, were included in these simulations.

Initial Conditions

The starting point for this series of simulations assumed a lizard-like reptile of 4 kg. mass. This was because (i) thermal inertia for an ectotherm of this size would enhance the importance of heating/cooling hysteresis and (ii) this was a size envisaged by Grigg (pers. com.) when considering the stepwise progression outlined in Grigg *et al.* (2004). It was given a standard metabolic rate (SMR) according to allometric equations cited in Withers (1992), that is 0.317 W when T_b was 20 °C. Its metabolic rate varied with body temperature according to a Q_{10} of 2.5. This commonly cited value for Q_{10} (Geiser 1988; Schmidt-Nielsen 1990) was retained throughout the study even though SMR was increased in subsequent simulations. A Q_{10} of 2.5 is consistent with that observed across a wide range of reptiles and mammals (White *et al.* 2006).

The overall thermal conductance (K_o) was calculated from the allometric relationships for the thermal time constant (τ) in both heating and cooling lizards as derived by Grigg *et al.* (1979). Thus, K_o was varied initially between 3.82 W·°C⁻¹ when cooling and 5.49 W·°C⁻¹ when heating.

Respiratory minute volume (V_i) for the virtual lizard was determined from the allometric equation cited by Withers (1992) for reptiles. Thus, V_i was 222 ml·min⁻¹ when M was 0.317 W. As M changed, V_i was varied in direct proportion.

Operative temperature (T_e) of the environment was varied daily between 15 °C and 45 °C for all simulations. Note that as T_e differs from air temperature due to the presence of insulation in particular, a T_e of 45 °C represented a daily opportunity to bask rather than a particularly hot day. Nonetheless, this temperature regime was warm compared to current global mean temperatures.

As the rate of evaporative cooling is determined by the absolute humidity gradient (not the relative humidity gradient), absolute humidity of the environment was calculated for 70 % saturation when air was at 15 °C and held constant. This implies that no day to day fluctuations of ambient absolute humidity were included in this study and renders daily fluctuations of relative humidity with temperature irrelevant.

Simulations

Note that while their step-wise model was used as a guide, the following simulations (and their numbers) do not necessarily coincide with stages 1 to 5 in the schema proposed by Grigg *et al.* (2004).

Note also that the starting points for the following simulations are often somewhat misleading. This is because thermal inertia in an animal of this size is important and lags result in the time course of T_b . Therefore analyses of the generated data were based on the second of two cycles of T_e fluctuation (from the second minimum to the third minimum) only. By the second “day” the T_b of the animal at all times was determined by its (thermoregulatory) history rather than by some arbitrary starting point.

Fifteen simulations were explored (approximately in sequence), as follows.

1. A virtual lizard with the physiological variables described above was placed in the virtual environment for 2 days (2880 minutes) from the time when T_e

was at its minimum (15 °C). It was allowed to adjust its thermal conductance so that it heated as fast as possible and cooled as slowly as possible, thus simulating heating/cooling hysteresis. The proportion of time spent within a nominal T_{pref} of 25 °C to 35 °C was noted for the second day.

2. The same animal was placed in the same environment as before, but this time it was allowed to adjust its K_o to maximise the time spent within T_{pref} . That is, K_o was minimal to minimise heat exchange with the environment while 25 °C < T_b < 35 °C. Outside this range, K_o was adjusted to quicken any approach to T_{pref} and to slow any departure from T_{pref} .
3. The animal from simulation 2 was given non-by-passable insulation to simulate the addition of an external coat of fur as discussed by Cowles (1946; 1958). That is, the minimum conductance was reduced to a value typical for mammals of this size according to allometric equations cited by Withers (1992). To conform to the concepts investigated by Cowles (1946; 1958), it was assumed that thermal conductance could be varied only in a restricted way. That is, the pelage lacked thermal windows and the degree of piloerection was more or less fixed, as would be the case for a lizard wearing a mink coat. To simulate this, K_o was allowed to vary only by the same factor as lizards of this size in general, that is, 1.4 fold between 0.665 W·°C⁻¹ and 0.931 W·°C⁻¹. The animal was then placed in the thermal environment fluctuating between 15 °C and 45 °C as before.
4. The animal from simulation 2 was given by-passable insulation so that K_o could be varied in a less restricted way. Grigg *et al.* (2004) envisaged a situation where subcutaneous fat layers combined with variable cutaneous perfusion would allow both effective basking and insulation in an otherwise ectothermic animal. In this study, this was simulated as a capacity to vary K_o six fold from its minimum value, which assumes (i) that the internal, sub-cutaneous insulation is as effective as pelage in modern mammals and (ii) that altering the cutaneous perfusion to by-pass the insulation has no more of an effect on K_o than altering the degree of piloerection and cutaneous perfusion to thermal windows in extant mammals. This seemed conservative given that *Homo sapiens* may vary K_o six-fold when immersed in water baths of different temperatures (Kleiber 1961) and large arctic mammals may vary their K_o as much as eleven-fold (Scholander, *et al.* 1950). Consequently, in this simulation, K_o was allowed to vary from 0.665 W·°C⁻¹ (Withers 1992) to 3.99 W·°C⁻¹ for the animal in the T_e fluctuations as before. SMR remained at lizard levels and the Q_{10} of 2.5 still pertained.
5. Grigg *et al.* (2004) proposed that locomotive activity in a lizard might contribute to facultative thermogenesis. This was simulated by allowing the animal in simulation 2 activity at any T_b > 25 °C, the lower limit of its T_{pref} . During activity, $M \geq 2.5$ W (say) which is about 5 times SMR for that T_b . Where SMR > 2.5 W due to the Q_{10} effect of T_b on SMR, the virtual animal's M was assumed to be SMR.
6. To investigate the possibility that locomotive activity might contribute to facultative thermogenesis once

by-passable insulation had evolved, the animal in simulation 4 was also allowed activity at any $T_b > 25^\circ\text{C}$ with $M \geq 2.5\text{ W}$ in the same way as in simulation 5.

7. An alternative to the heat produced by activity might be the heat produced by shivering thermogenesis (Grigg, *et al.* 2004). Therefore, the animal from simulation 2 was given a thermogenic capacity which was initiated when T_b fell below the preferred range of 25°C to 35°C . Thus, M was set to that value required to maintain T_b within, or to raise T_b to, T_{pref} . However, maximum thermogenesis was set to 5 W , equivalent to giving the animal an aerobic scope of 10. If the thermogenesis required to attain or maintain T_b was greater than this maximum, then no thermogenesis was initiated. This reflects the assumption that natural selection may act against individuals that spend energy without success.
8. In this simulation an animal that had evolved by-passable insulation but still with lizard SMR (simulation 4) was allowed thermogenesis to a maximum of 5 W as per simulation 7. Again, this thermogenesis was initiated only when $T_b < 25^\circ\text{C}$ and when it was sufficient to maintain or attain $T_b > 25^\circ\text{C}$.
9. In this and the following two simulations, SMR was increased incrementally to reflect increasing leakiness of cell membranes. For this sequence of simulations, it was assumed that the animal had evolved by-passable insulation, as well as shivering thermogenesis which was limited by an aerobic scope of 10. An animal with high SMR and no insulation is simulated later. Thus, for this simulation, the animal in simulation 8 was given SMR of 0.4 W and a V_i of $280\text{ ml}\cdot\text{min}^{-1}$ at $T_b \sim 15^\circ\text{C}$ ($T_e = 15^\circ\text{C}$). A Q_{10} of 2.5 dictates that SMR was about 1 W when $T_b \sim 25^\circ\text{C}$ and an aerobic scope of 10 means that maximum thermogenesis was therefore 10 W . As with all other simulations, T_e varied between 15°C and 45°C on a daily basis for 2880 minutes, humidity was 70% when air temperature was 15°C and data from "day 2" only were analysed.
10. In this simulation the animal in simulation 9 was given double SMR such that $\text{SMR} = 0.8\text{ W}$ and $V_i = 500\text{ ml}\cdot\text{min}^{-1}$ at $T_b \sim 15^\circ\text{C}$ and maximum M was 20 W . K_o varied between $0.665\text{ W}\cdot^\circ\text{C}^{-1}$ and $3.99\text{ W}\cdot^\circ\text{C}^{-1}$; unchanged from simulation 9 (as well as simulation 8 and 4).
11. In this simulation the SMR was doubled again such that $\text{SMR} = 1.6\text{ W}$ and $V_i = 1000\text{ ml}\cdot\text{min}^{-1}$ at $T_b \sim 15^\circ\text{C}$. Thermal conductance remained unchanged from simulation 4. However, as a $T_b \geq 25^\circ\text{C}$ was maintained throughout the second day in simulation 10 (see Results), T_{pref} was narrowed in this simulation. Here T_{pref} ranged from 30°C to 35°C and the shivering thermogenesis was initiated when T_b dropped below 30°C . This step towards homeothermic endothermy implies that there was a benefit to the animal from physiological rates being optimal in a narrower range of T_b . Presumably, this benefit outweighed the costs incurred by spending less time each day within T_{pref} .
12. The trend towards homeothermy progressed in this simulation where T_{pref} for the animal in simulation 11 was further narrowed to 34°C to 35°C . Thermogenesis

sufficient to maintain T_{pref} was initiated at a T_b of 34°C as long as the aerobic scope of 10 (40 W) was not exceeded. Other parameters, such as SMR, V_i , K_o range remained unchanged from simulation 11.

13. The SMR in simulation 12 was about eight times that for simulations 1 to 8. Such an increase is commensurate with the differences in SMR between extant lizards and mammals of the same size (Bennett, 1991; Withers 1992). However, under the conditions specified, T_b was not maintained all "night" unlike in some previous simulations (see Results and Discussion). This was attributed to the constraints imposed by a combination of the SMR used and the aerobic scope of 10. Therefore, SMR was increased marginally in this simulation to 2 W at $T_b \sim 15^\circ\text{C}$ or a little less than 10 fold the original SMR. Consequently, V_i was increased to $1200\text{ ml}\cdot\text{min}^{-1}$ and maximum M was increased to 50 W (10 times the SMR at $T_b = 25^\circ\text{C}$). Thermal conductance remained unchanged.
14. To investigate the predicted thermoregulation of an animal with mammalian metabolic rates and reptilian thermal conductance, the animal from simulation 13 was given a K_o ranging from $3.82\text{ W}\cdot^\circ\text{C}^{-1}$ to $5.49\text{ W}\cdot^\circ\text{C}^{-1}$ as per simulation 2.
15. So far, no effect of turbinal scrolls had been included. To investigate any possible advantages turbinal scrolls might impart in this warm, mesic environment, the expired air for the animal in simulation 13 was reduced by (an arbitrary) 5°C throughout this simulation ($T_{ue} = 5^\circ\text{C}$).

For all simulations the times spent within T_{pref} were calculated (using data from the second day only) and reported as number of minutes as well as percentage of the day. In some cases thermogenesis resulted in T_b that were almost, but not quite, within T_{pref} . In these cases the times spent within one degree of T_{pref} were also calculated. Additionally, the effectivenesses of thermoregulation *sensu* Hertz *et al.* (1993) (E_j) were also calculated.

Results

Simulations

1. Body temperature of the initial lizard-like virtual animal closely followed T_e throughout the (second) day (Figure 1): $E_j = 0.0372$ (Table 1). The environment was the major source of heat during heating and the major sink during cooling (Figure 1). Heat was exchanged rapidly with the environment as K_o was high, being typical for lizards. However K_o was regulated so that the animal cooled more slowly than it heated inducing the heating cooling/hysteresis and the different time lags between T_b and T_e . Metabolic heat was only a minor element in the heat budget of this animal and varied with T_b due only to the Q_{10} effect. Evaporative cooling varied with M : there being a link between M and V_i as well as an increased saturation of expired air at high T_b . In this simulation, E more than compensated for M at high T_b and $T_e \sim 45^\circ\text{C}$ (the highest T_e) throughout. The animal spent 22 % of the day with T_b between 25°C and 35°C (Table 1).

Table 1. Effects of adjustments in thermal conductance (K_o) and metabolic rate (varying SMR and adding activity or thermogenesis) on the time (t in minutes and as a percentage of the day) spent within given preferred range (l to u) of T_b (T_{pref}) and the effectiveness of thermoregulation (E_f) for a 4 kg animal simulated at various proposed stages in the evolution of endothermy in a thermal environment where operative temperature (T_o) fluctuated daily between 15 °C and 45 °C. Data on the left derive from an animal with high lizard-type thermal conductance; data of the right derive from an animal with low mammalian-type thermal conductance.

Low insulation / high thermal conductance					High insulation / low thermal conductance				
Sim	Features	T_{pref}	E_f		Sim	Features	T_{pref}	E_f	
l (°C) u (°C) t min t %					l (°C) u (°C) t min t %				
1	heating / cooling hysteresis	25	25	320 .0372					
2	l + adjusts K_o to maximise time in T_{pref}	25	35	360 .0514	3	2 + non-by-passable insulation	25	35	660 .4759
					4	2 + by-passable insulation	25	35	750 .4980
5	2 + activity at 5 × SMR	25	35	350 .0624	6	4 + activity at 5 × SMR	25	35	840 .4950
7	2 + thermogenesis upto 10 × SMR	25	35	360 .0514	8	4 + thermogenesis up to 10 × SMR	25	35	760 .4908
					9	8 + 2 × original SMR	25	35	780 .5190
					10	8 + 4 × original SMR	25	35	1060 .4844 (1100) (.4824)
					11	8 + 8 × original SMR: T_{pref} begins to narrow	30	35	920 .5156 (1010) (.4518)
					12	11 + T_{pref} narrowed further: thermogenesis ceased late at night	34	35	150 .5156 (360) (.4615)
14	2 + thermogenic capacity: 10 × original SMR	25	35	340 .1255	13	12 but 10 × original SMR	34	35	570 .5870 (860) (.4529)
					15	13 + turbinal scrolls	34	35	540 .4969 (770) (.3675)

2. Adjusting K_o to maximise the time spent within T_{pref} increased the effectiveness of thermoregulation marginally to $E_f = 0.0514$ and the time spent within T_{pref} to 25 % of the day (Table 1). However, metabolic heat was still a minor element of the heat budget and T_b was dictated predominantly by fluctuations in T_e : the animal was still essentially a thermoconformer (Figure 1).
3. Adding non-by-passable insulation significantly increased the time spent in T_{pref} to 46% of the day and E_f to 0.4759 (Table 1). Time lags for both heating and cooling of the animal were substantial so that T_{pref} was not attained until 400 minutes after the occurrence of minimum T_e (Figure 2). T_{pref} was maintained until 10 minutes after the maximum T_e after which T_{pref} was exceeded for another 390 minutes. On the other hand, the time lag ensured that T_{pref} was maintained through the rest of the “night” until 10 minutes before the minimum T_e . Heat balance was still dominated by sensible heat exchanged with the environment.
4. With by-passable insulation, T_{pref} was reached sooner in the day as heat was absorbed more rapidly from the environment when thermal conductance was high (Figure 2). Thus, T_{pref} was achieved 330 minutes after the minimum T_e , an hour earlier than when insulation was non-by-passable. Similarly T_b exceeded T_{pref} for 340 minutes during the day, nearly an hour less than when insulation was non-by-passable (simulation 3). As a result, the animal spent more (52 %) of its day within T_{pref} with a higher E_f (0.4980) than when insulation was non-by-passable (Table 1).
5. For an animal with reptilian thermal conductance (as in simulation 2), increasing and prolonging metabolic heat production through activity did not increase the time spent within T_{pref} although it did increase E_f slightly to 0.0624 (Table 1). In the circumstances of this simulation, evaporative heat loss exceeded metabolic heat production, especially at high T_b where saturated expired air carried more evaporated water (Figure 1).
6. However, for an animal with mammalian thermal conductance (as in simulation 4), increasing and prolonging metabolic heat production through activity increased the time spent within T_{pref} to 58% of its day, although it decreased E_f very marginally to 0.4950 (Table 1).
7. Giving the animal with reptilian K_o (in simulation 2) a capacity for shivering thermogenesis with an aerobic scope of 10 had no effect on time spent within T_{pref} or on E_f (Table 1). No thermogenesis was initiated by the algorithm which included the constraint that thermogenesis should occur only if it resulted in T_b being raised to T_{pref} .
8. Similarly, giving the animal with by-passable insulation (simulation 4) a capacity for shivering thermogenesis, again with an aerobic scope of 10, had very little effect on its thermoregulation (Table 1). Time spent within T_{pref} increased by 10 minutes (which, given the 10 minute precision of the modelling, is not significant) while E_f decreased marginally (Table 2).
9. Doubling the SMR of the animal with by-passable insulation and rudimentary thermogenic capacity (simulation 8) increased the time spent in T_{pref} to 780 minutes or 54 % of the day) and E_f to 0.5190 (Table 1). For the first time, readily identifiable thermogenesis was initiated, once just before “mid-morning” as T_b increased towards T_{pref} and once during the “night” as T_b fell below T_{pref} (Figure 2). However, these spikes in metabolic rate were short-lived. The environment still represented the major heat source for the animal while it warmed and metabolic heat was still a minor element of the heat budget.
10. Doubling SMR again while maintaining the aerobic scope of 10 resulted in significant thermogenesis “overnight” with T_b maintained more or less in T_{pref} : minimum T_b was 24.94 °C during this thermogenesis. Consequently, the only real departures of T_b from T_{pref} were those where T_b exceeded the upper limit of T_{pref} in the absence of various cooling mechanisms in these simulations. T_b was within T_{pref} for 1060 minutes (74 %) of the day and between 24 °C and 35 °C for 1100 minutes (76 %) of the day. The decrease in E_f to 0.4844 may have been due to changes in variance in the distribution of T_b (Hertz, *et al.* 1993). Such changes resulted from a reduction in the frequency of $T_b < T_{pref}$ on the one hand, but, because of the lack of cooling mechanisms, no significant effect on the frequency $T_b > T_{pref}$ on the other. In this simulation, the increased M assumed a significant role in the heat budget of the animal throughout the day (Figure 2). Heat produced by metabolism and heat absorbed from the environment were, at different times, nearly equal.
11. In simulation 10 sufficient heat was produced to maintain T_b more or less greater than 25 °C throughout the day. Doubling the SMR in simulation 11 was sufficient to maintain T_b more or less above 30 °C (minimum T_b was 29.92 °C) with significant thermogenesis initiated when required (Figure 2). Consequently, narrowing the T_{pref} did not contribute to the reduction of time spent with T_b between 30 °C and 35 °C (920 minutes or 64%) or between 29 °C and 35 °C (1010 minutes or 70%: Table 1). Such a decrease of time in T_{pref} correlates with the higher T_b above T_{pref} associated with higher SMR. E_f increased once again to 0.5156. By this stage metabolic heat production and evaporative heat loss dominated the heat budget of the animal with sensible heat exchanged with the environment having become relatively minor throughout (Figure 2).
12. Narrowing T_{pref} further to the range 34 °C to 35 °C without further increases in SMR or aerobic capacity resulted in T_b not being maintained throughout the day (Figure 2). T_b was maintained during the early part of the “night”. Thereafter, as M reached its maximum (40 W), T_{pref} could not be maintained, M ceased and T_b was allowed to fall until such time as the environment became a heat source. At this time, T_b increased due to sensible heat absorbed from the environment. This

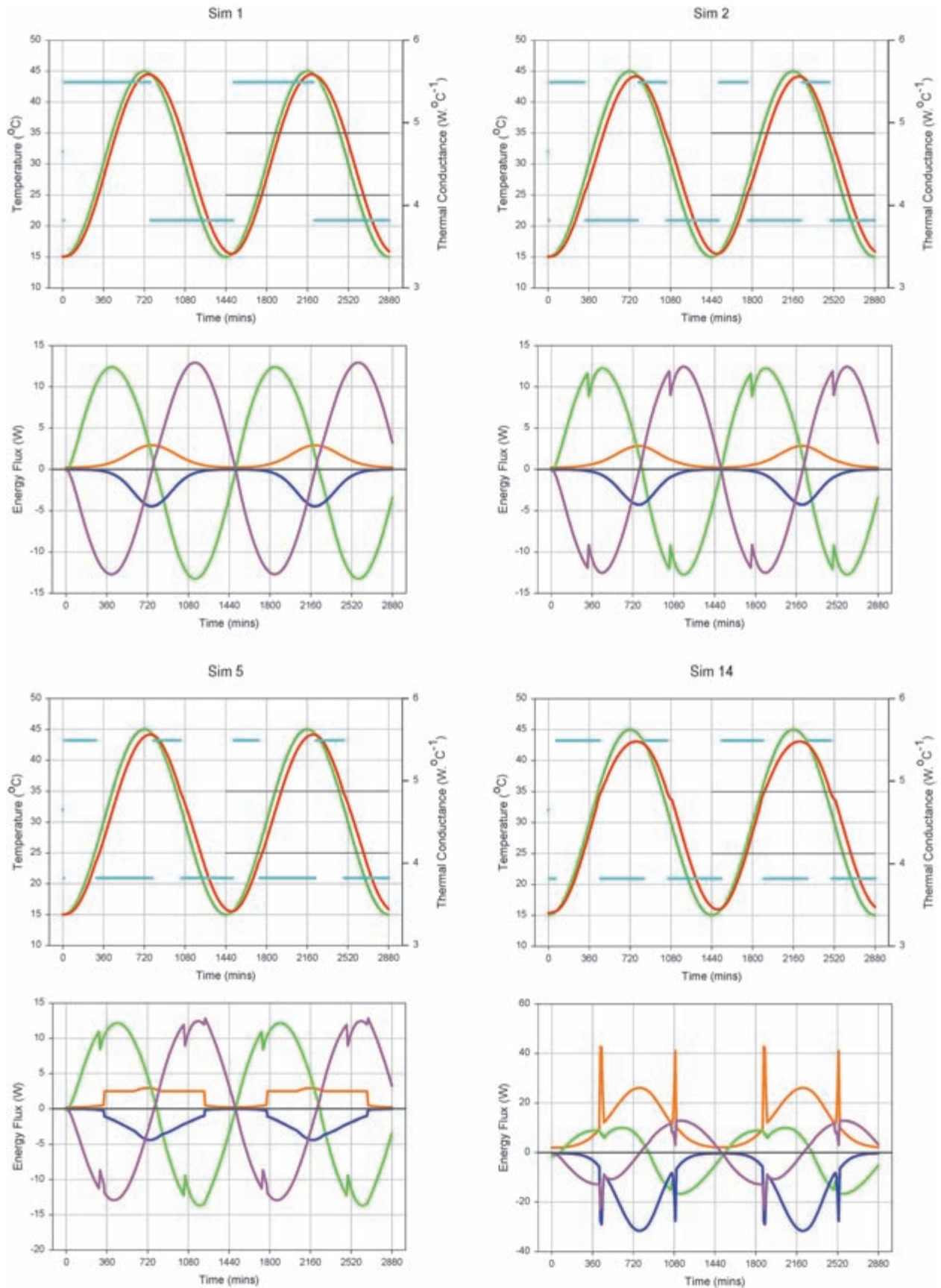


Figure I. Body temperature and energy flux resulting from selected simulations (numbered as in Table 1 and Methods) of a 4 kg animal with high lizard-like thermal conductance. For each simulation, the upper panel depicts T_e (green line), T_b (red line), K_o (blue line) and T_{pref} (between thin black lines) and the lower panel depicts M (red line), E (blue line), sensible heat exchange with the environment (green line) and heat exchange with the body store (magenta line). Data derived from simulations over two daily T_e fluctuations but were analysed only from the second cycle. See text for more details.

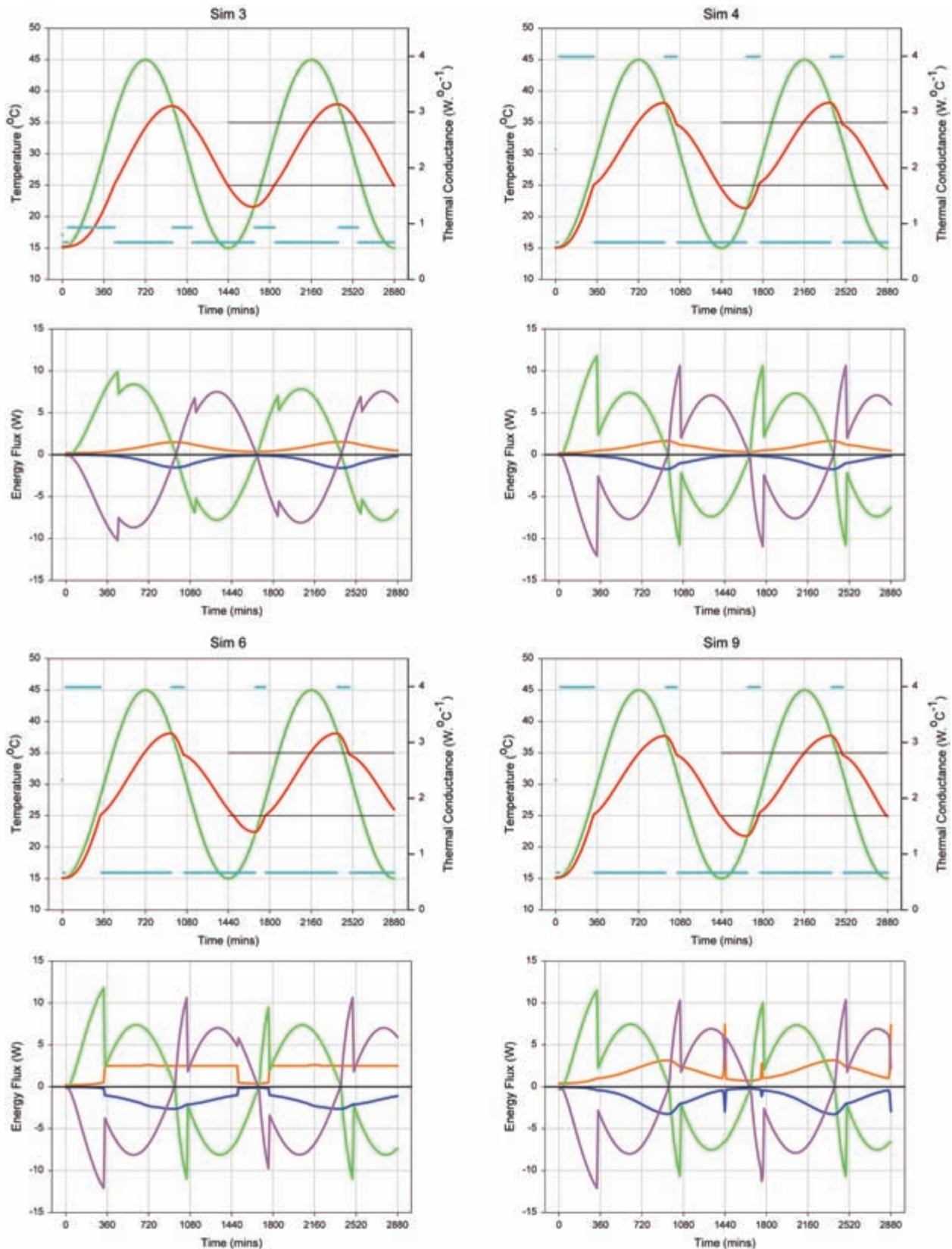


Figure 2. Body temperature and energy flux resulting from selected simulations (numbered as in Table 1 and Methods) of a 4 kg animal with low mammal-like thermal conductance. For each simulation, the upper panel depicts T_e (green line), T_b (red line), K_o (blue line) and T_{pref} (between thin black lines) and the lower panel depicts M (red line), E (blue line), sensible heat exchange with the environment (green line) and heat exchange with the body store (magenta line). Data derived from simulations over two daily T_e fluctuations but were analysed only from the second cycle. See text for more details.

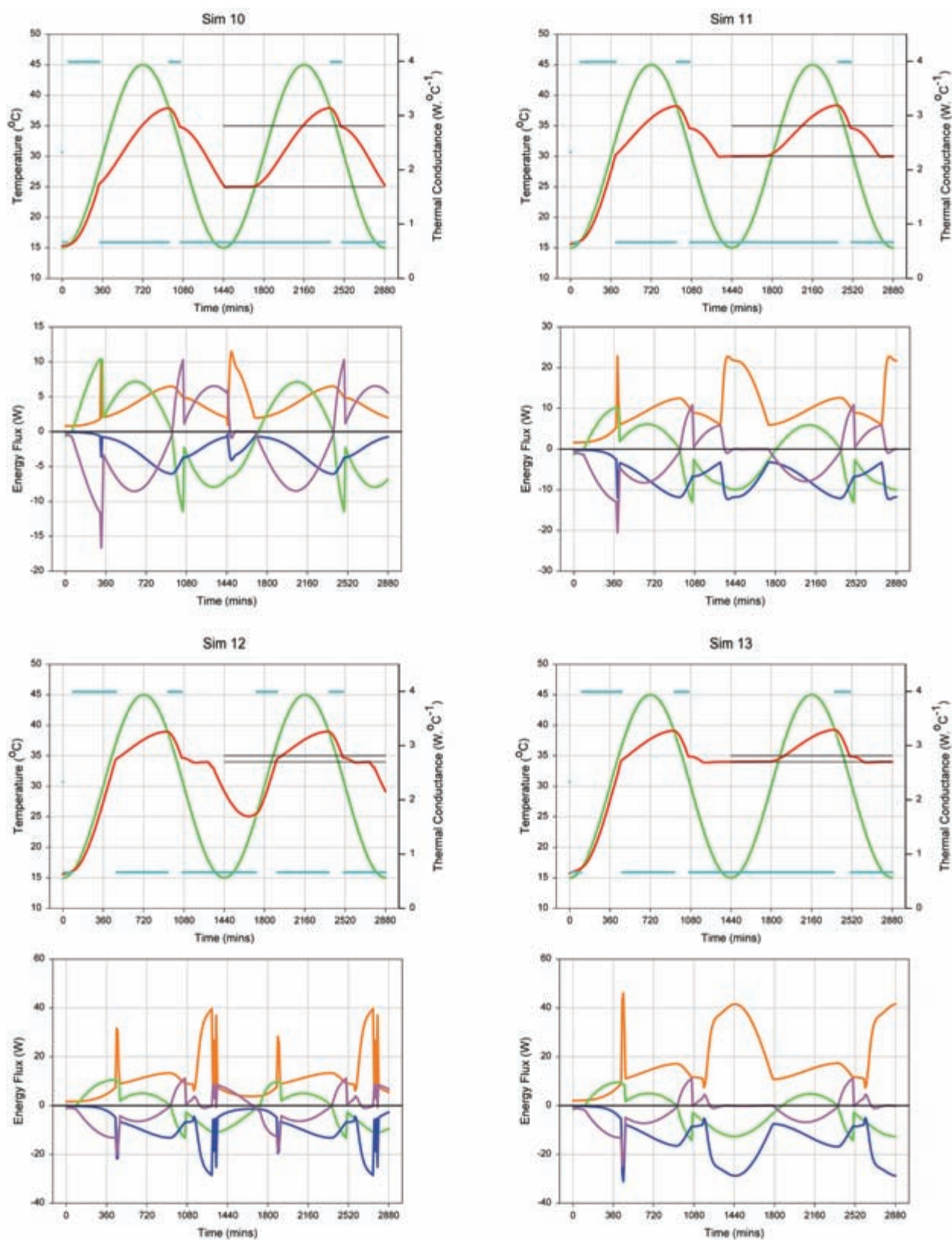


Figure 2 continued.

was supplemented by a short spike of (intense) shivering thermogenesis until T_b returned to T_{pref} once again. Therefore, only 360 minutes (25 %) were spent with T_b between 33 °C and 35 °C; 150 minutes (10 %) of the day within T_{pref} (Table 1).

13. Increasing SMR to about 10 times the original while maintaining the aerobic scope of 10 was sufficient to maintain T_b at least above 33.88 °C (T_{pref} was 34 °C to 35 °C) all “night” (Figure 2). 860 minutes (60 %) of each day were spent with 33 °C < T_b < 35 °C. Failures in thermoregulation were due to the time T_b spent above T_{pref} . E_f was 0.5870 (34 °C to 35 °C) indicating the closest approach to a perfect thermoregulator (when $E_f = 1$) so far. This thermoregulation was particularly apparent from the relationship between T_b and T_e (Figure 3). The relationship between M and T_e for this animal in these circumstances revealed the magnitude of shivering thermogenesis increasing at $T_e < \sim 28$ °C. There is a zone of T_e between ~ 28 °C and ~ 32 °C where M is nearly constant. This pattern, purely an emergent property of the modelling, is reminiscent of the pattern exhibited by a classical endotherm, in this case, one with a basal metabolic rate (BMR) of ~ 11 W. Above a T_e of about 32 °C (and in the absence of cooling mechanisms) two values of M and T_b pertained for any given T_e . This was due to the cyclically fluctuating thermal environment preventing the animal with significant thermal inertia ever reaching equilibrium. That is, for any given $T_e >$

~ 32 °C, one value derived from the time lag between T_e and T_b in a cooling thermal environment, the other in a warming one. This was in contrast to experimental data from classical endotherms that are normally collected in stable (laboratory) thermal environments.

14. The animal with high “mammalian” SMR but with reptilian or lizard values for thermal conductance was unable to retain its heat: T_b remained largely coupled to T_e throughout the cycle despite prodigious amounts of metabolic energy used, including during periodic (but short-lived) attempts at thermogenesis (Figure 1). Even for a wide T_{pref} of 25 °C to 35 °C, E_f was low (0.1255) with time spent within this range not exceeding that for the same animal with low (reptilian) SMR (Table 1).
15. Giving the animal in simulation 13 turbinal scrolls that reduce the temperature of the expired air by 5 °C throughout ($T_{ue} = 5$ °C) substantially reduced the amount of energy needed to maintain T_{pref} through the “night”, although it increased M when T_e is high (Figure 3). The reduction in M at low T_e was associated with the substantial reduction in E as expired air at lower temperatures held less water vapour. As well as reducing M at low T_e , adding the turbinal scrolls altered the “thermal neutral zone” to between 26 °C and 30 °C (Figure 3). As a result of the increased M at high T_e and therefore the associated increased T_b , E_f and time spent within T_{pref} were actually lowered (Table 1).

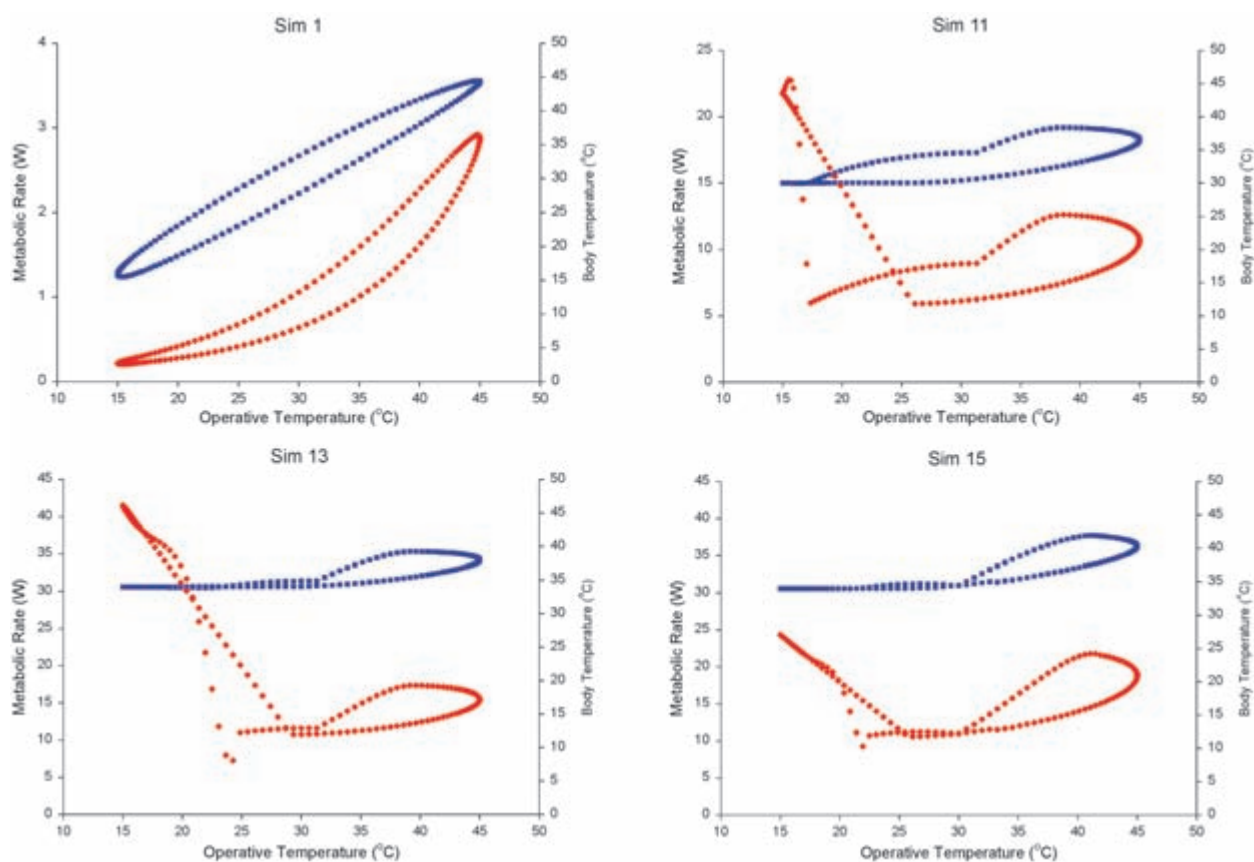


Figure 3. Body temperature (blue points) and metabolic rate (red points) as functions of operative temperature from selected simulations showing the emergence of a thermal neutral zone and basal metabolic rate in the proposed sequence from thermoconforming ectothermy to thermoregulating endothermy. Cooling mechanisms were absent precluding thermoregulation above thermoneutrality and operative temperature fluctuated preventing the attainment of steady state.

Discussion

Quantitative exercises such as this provide insight into qualitative explanations for the evolution of endothermy. By assuming that maximising time within some preferred body temperature range is advantageous and by using heat budget modelling to predict body temperature, this exploratory study has demonstrated the in principle feasibility of deriving a medium sized mammal-like endotherm from an ectothermic lizard-like precursor. Similar exercises might be used to (i) examine a variety of proposed models for the evolution of endothermy, (ii) examine and compare the feasibility of the evolution of endothermy in a variety of thermal environments and/or (iii) examine and compare the feasibility of such evolution for animals over a range of size classes. Since the quantitative modelling presented here is versatile (Brice 2008) this approach may be used for all these purposes. This is but an initial study.

Here, the quantitative modelling was applied to a specific qualitative model for the evolution of endothermy, namely that proposed by Grigg *et al.* (2004). In fact, it really only addressed a number of the issues raised. These included hypotheses that by-passable insulation predated high SMR, that activity or shivering thermogenesis, even in animals with a low SMR and high K_o , have benefits in terms of maintaining T_b , and that torpor is plesiomorphic in endotherms. By emulating some of the stages proposed by Grigg *et al.* (2004), the study provided support for two out of three of these, at least in the limited circumstances investigated.

It is clear that in these circumstances, heat generated by high M would be lost to the environment if endotherms retained K_o typical of many ectotherms. The modelling predicted no increase in time spent within T_{pref} as a result of heat generated either by moderately sustained activity (simulation 5) or by thermogenesis up to ten times SMR (simulation 7). A ten-fold increase of SMR itself, coupled with a capacity for thermogenesis, also failed to increase the time spent in T_{pref} (simulation 14). Only with insulation reducing minimum thermal conductance was heat retained enough to benefit the modelled animal's thermoregulation. The benefits of the insulation were quantifiable, both in terms of time spent in T_{pref} and in terms of E_r . The existence of insulation alone increased time in T_{pref} by five hours, six and half if the insulation was by-passable (simulations 2, 3 and 4). There were other benefits to the insulation being by-passable that were not so apparent from the data. By-passing the insulation allowed the animal to gain heat more rapidly when the environment was a heat source. That is, by basking the animal could reach its T_{pref} an hour earlier in the morning. Presumably, this would have given it advantages, such as reduced vulnerability to predation, and access to resources earlier than animals with less variable thermal conductance. Whether by-passable or not, insulation alone seemed to confer more thermoregulatory benefits to animals than increased metabolic rate alone, at least in the circumstances modelled. This raises obvious questions about the lack of insulation in extant ectotherms. Presumably, this modelling was too constrained to explain the continued success of animals without effective

insulation. There is scope to expand these sorts of studies to consider the thermoregulation of animals in different environments, including those where mosaics of different T_e regimes provide for efficient behavioural thermoregulation. What this study did show, though, was that without the insulation, heat generated endogenously was rapidly lost to the environment.

Two sources of endogenous heat were investigated, heat from activity and heat from shivering thermogenesis. In this modelling, activity was constrained by the requirement that it occur only while T_b was within T_{pref} . It was assumed that at $T_b < T_{pref}$ the animal was lethargic and unable to be vigorous. Thus, activity could be no substitute for thermogenesis when the animal was cold, and this would have mitigated against activity as a useful thermoregulatory strategy. The constraint was included in the modelling to include the implications of lethargy, and was an attempt at realism. Nonetheless, once T_{pref} was attained (through sensible heat exchange with the environment), activity was expected to prolong the time spent within this range (at the end of the day). This occurred only when K_o was low (simulation 6), when the heat generated by activity was not immediately lost to the environment. Activity in a virtual animal with by-passable insulation increased its time in T_{pref} by 90 minutes compared to one in which there was no activity.

Neither was any degree of shivering thermogenesis facultative when thermal conductance was high, at values typical for lizards (simulations 7 and 14). Even with the lower thermal conductance values typical for mammals, the capacity for thermogenesis was futile while SMR was low (simulation 8). Small increases in SMR had little effect over and above that conferred by insulation alone (simulation 9). Only once SMR had quadrupled was there any substantial increase in time spent in T_{pref} . This was due to another deliberate constraint in the modelling. Aerobic scope was limited to 10 throughout, a value typical in lizards and mammals (Bennett 1991). Increasing M (as measured when $T_b \sim 25^\circ\text{C}$) ten-fold, to the aerobic limit, was insufficient to maintain T_b until SMR itself increased four-fold. Because inefficient energy use was considered disadvantageous, thermogenesis that would have been unsuccessful at maintaining T_{pref} was not attempted by the virtual animal at any stage. Consequently, no further advantage (over the presence of insulation) accrued until SMR had increased substantially.

The thermal biology of at least two extant vertebrate families challenges these results. In the first case, Tachyglossidae have SMR about a quarter to a third that of eutherian mammals (Dawson, *et al.* 1979), yet they are capable of maintaining high and stable $T_b \geq 30^\circ\text{C}$ in the laboratory (Schmidt-Nielsen, *et al.* 1966) and in the field (Beard and Grigg 2000). They may be able to achieve this because of their particularly low minimum thermal conductance. Recent data show that echidnas may be able to reduce K_o to half that predicted for other mammals of their size (Brice 2008). In the second family, the Boidae, brooding female pythons provide heat for their eggs through shivering thermogenesis, or its analogue (Hutchison, *et al.* 1966; van Mierop and Barnard 1978; Harlow and Grigg 1984). What is surprising for these squamates, is that female pythons

are able to maintain T_b ($30\text{ }^{\circ}\text{C} \pm 3\text{ }^{\circ}\text{C}$) that are up to $7\text{ }^{\circ}\text{C}$ warmer than ambient in the laboratory (Harlow and Grigg 1984) and up to $9\text{ }^{\circ}\text{C}$ (or more) warmer than ambient in the field (Slip and Shine 1988). Two features probably facilitate brooding boid thermoregulation: lower than expected thermal conductance and higher than expected aerobic scope. Ellis and Chappell (1987) showed that thermal conductance in a cooling 1.5 kg ball python (*Python regius*) is a third of that expected in a 1.5 kg lizard (based on Grigg *et al.* 1979). Thermal conductance, calculated (as the ratio of oxygen consumption to gradient between body and ambient temperature) in a 21 kg brooding Indian python (*Python molurus bivittatus*) (van Mierop and Barnard 1978), is only slightly more than a quarter that expected in a similar-sized cooling crocodilian (Smith 1976; Johnson, *et al.* 1978). Although thermal conductance calculated from metabolic and temperature data may not always be equivalent to that calculated from cooling curves (Smith 1976; Johnson, *et al.* 1978; Grigg, *et al.* 1979), these data suggest that over a wide range of sizes, brooding (and non-brooding (van Mierop and Barnard 1978)) boids have substantially lower K_o than lizard-shaped ectotherms of similar mass. Presumably, this is due in part to their posture. By coiling, boids can reduce their surface area to volume ratio substantially.

Low as it may be, boid minimum K_o are still approximately double that of similar sized mammals. Boid SMR are < 0.1 that expected for similar-sized mammals (Hutchison, *et al.* 1966; Harlow and Grigg 1984). For this combination of K_o and SMR, the modelling suggests that thermogenesis would be ineffective at maintaining T_b . That boids can maintain T_b against $> 5\text{ }^{\circ}\text{C}$ gradients to ambient may be due to relatively high aerobic scopes. While the modelled animal was constrained by an aerobic scope of 10, Harlow and Grigg (1984) report an oxygen consumption while brooding 22 times that while not (at the same temperature) in diamond pythons (*Python spilotes spilotes*). Reported postprandial metabolic rates as high as 44 times SMR (Secor and Diamond 1997) suggest the capacity for even higher aerobic scope in Burmese pythons (*Python molurus*). Nonetheless, thermogenesis in boids appears to fail at T_e as low as the minimum modelled ($15\text{ }^{\circ}\text{C}$). Oxygen consumption peaks at $24\text{ }^{\circ}\text{C} < T_a < 27\text{ }^{\circ}\text{C}$ and declines at lower T_a (Hutchison, *et al.* 1966; van Mierop and Barnard 1978). While not yet included, there is potential to investigate further the thermal ecology of boids with this modelling approach.

Unexpectedly, support for plesiomorphic daily torpor emerged from the modelling in this study (simulation 12). With SMR increased 8-fold over the initial simulation, and with an aerobic scope of 10, the virtual animal was unable to maintain T_b within (the narrowed) T_{pref} all night. Thermogenesis was able to maintain T_{pref} during the early part of the night, but once T_e dropped to near minimum, this ceased and M and T_b declined. Next “morning”, increasing T_e provided the opportunity to bask. This, supplemented by a (short) bout of thermogenesis, facilitated the return of T_b to T_{pref} . This pattern of activity in the early part of the night followed by torpor later is seen in a number of mammalian daily heterotherms (Audet and Fenton 1988; Song, *et al.* 1995; Song, *et al.* 1997; Geiser 2004). Further, at least mouse lemurs (*Microcebus murinus*) use increases in ambient temperature to increase body temperature

(Ortmann, *et al.* 1996), while fat-tailed dunnarts *Sminthopsis crassicaudata* and Giles’ planigales (*Planigale gilesi*) bask during the morning (Warnecke, *et al.* 2006). In the modelled animal, daily torpor was the result of its circumstances. These included the particular T_e regime simulated, the range of T_{pref} and the maximum thermogenic capacity. Once again, aerobic scope was implicated. It should be noted though, that here, aerobic scope was a constraint which did not interact directly with natural selection. The endotherm here evolved in response to selection acting to increase its time within T_{pref} , not overtly in response to any factor acting on aerobic scope. This differs from the aerobic capacity model in which natural selection acts on aerobic endurance (Bennett 1991). In the aerobic capacity model, advantages are seen to accrue to animals that extend their maximum metabolic rate, which in turn correlates to an increase in SMR. Bennett (1991) pointed out that it is not clear why SMR should increase in proportion to maximum M , though by doing so an aerobic scope of about ten is conserved across classes. Here, aerobic scope was assumed to be due to some intrinsic, unspecified limits that pertain to both ectotherms and endotherms (for possible examples see Weibel, *et al.* 1998) such that it is conserved across classes. By selecting for time in T_{pref} instead of aerobic capacity, this study demonstrated how endotherms might have evolved from ectotherms purely by increasing capacity for physiological thermoregulation. Because aerobic scope was a limit, one stage was characterised by daily torpor at the particular regime for T_e and T_{pref} selected. As well, aerobic scope also prevented sufficient thermogenesis at earlier stages when SMR was closer to reptilian values than to mammalian values. Thus, in this study, aerobic scope emerges as a significant factor in thermoregulation and the evolution of endothermy, not unexpectedly, but in a different role from that proposed in some models.

Also emerging from the final stages of this modelling were various thermoregulatory features found in extant endotherms, at least in a qualitative way. These included the “basal metabolic rate” or BMR which was exhibited over a range of T_e defining the “thermal neutral zone” or TNZ (Figure 3). Both the BMR and the TNZ are characteristic of the Scholander model of endotherm thermoregulation (Scholander, *et al.* 1950). Both emerged from the modelling in this study without any specific inputs to define them. Initially, with low SMR, no thermogenesis and only heating/cooling hysteresis to control T_b , the modelled animal was a thermoconformer (Simulation 1). T_b varied above and below T_e only because of the time lags induced by the thermal inertia. As T_b (nearly) tracked T_e and because of the effect T_b had on M , metabolic rate varied as expected for such a thermoconforming ectotherm. With the advent of insulation, a thermogenic capacity and incremental increases in SMR, the proto-endotherm was able to maintain T_b within T_{pref} at lower T_e (Figure 3, simulations 11, 13 and 15). Note that while T_{pref} was still relatively wide ($30\text{ }^{\circ}\text{C} < T_{pref} < 35\text{ }^{\circ}\text{C}$) there was a zone, $26\text{ }^{\circ}\text{C} < T_e < 31\text{ }^{\circ}\text{C}$ where two values for M were associated with the maintenance of T_{pref} : $M \sim 6\text{ W}$ when $T_b = 30\text{ }^{\circ}\text{C}$ and $M \sim 9\text{ W}$ when $T_b = 35\text{ }^{\circ}\text{C}$ (simulation 11). As T_{pref} narrowed further, these two values for M approached each other until a pattern reminiscent of a classical endotherm emerged (simulation 13). The TNZ

emerged ultimately as a result of the combination of the wide range of K_o and the narrow range of T_{pref} , and BMR was the M required to maintain this T_{pref} . Above the TNZ, T_b was less controlled and more variable because of the lack of cooling mechanisms and the fluctuating thermal environment. Consequently, M was variable due to the temperature effect imposed by these variations in T_b .

As well as the similarities between this virtual animal and extant endotherms, there were important differences. For example, BMR was higher than expected for a modern mammal (Withers 1992). Likely reasons may relate to anatomical features of the mammalian respiratory tract not incorporated in the modelling. The derived virtual endotherm had a respiratory minute volume increased (more or less) in direct proportion to the ten-fold increase in SMR modelled, rather than one typical of mammals of its size. If the anatomy of the mammalian lung evolved to increase the efficiency of oxygen exchange, then perhaps the lack of these adaptations may have resulted in elevated BMR. Also implicated by the simple virtual lung may be increased evaporative water loss. By being obliged to exchange an inflated volume of air, the virtual animal may have been losing excess evaporative water, and therefore evaporative heat. To maintain T_{pref} such an animal would likely need an increased BMR to compensate. Differences between the respiratory anatomy assumed here and that in extant mammals may translate to differences in V_i . Therefore, use of the modelling approach in this study would allow further investigation into such effects, although these were not included here. What was included, in a rudimentary way, was the effect of turbinal scrolls on the thermoregulation of the contrived endotherm. The inclusion of turbinal scrolls, through the simple and arbitrary reduction in temperature of expired air, had a marked and measurable effect on M . This occurred through the reduction of evaporative heat loss and the consequent saving in shivering thermogenesis necessary to balance sensible heat loss to the environment

(Figure 3 simulation 15). It is notable that these benefits were substantial, even for an endotherm in the warm, mesic environment simulated. Turbinal scrolls are often cited as adaptations for saving heat and/or water (Hillenius and Ruben 2004) implying perhaps that they may not be so necessary when the environment is neither cold nor dry. Adding sophistication, such as allowing T_{ue} to vary in different circumstances is likely to provide further insight into endotherm thermoregulation in a variety of habitats. Additionally, some cooling mechanisms, such as panting, were denied to the virtual animals. While panting occurs in both reptiles and mammals, it was excluded in these initial simulations for the sake of simplicity. If the metabolic costs of panting were known, as well as the V_i during panting, then this cooling could also be incorporated easily into the modelling. There is great potential to extend a study such as this to investigate a wide variety of adaptations to both the heat and the cold.

Although somewhat exploratory and lacking in detail, this study has provided a number of useful insights into the possible evolution of endothermy as proposed in one model. It has provided quantitative, if virtual, support for some, but not all, hypotheses deriving from a qualitative model. However, the scope of this study is still limited to one particular sized animal in one particular environment. To be comprehensive, the conclusions drawn here need also to derive from multiple studies that include a variety of feasible thermal environments and variously sized animals. The quantitative modelling approach used here is versatile enough to achieve this. It is also versatile enough to incorporate at least panting, class specific differences in respiratory minute volume and variable effects of turbinal scrolls in the physiology of any virtual animal. It may also be utilised to investigate a number of other models proposed for the evolution of endothermy. Consequently, substantial further study is necessary, and feasible, to address and extend the current debate about the evolution of endothermy.

Acknowledgements

This paper was presented at a symposium to mark the retirement of Professor Gordon Grigg in 2007. Consequently, I hope the usual team, Lyn Beard, Janette Donovan, Robbie Wilson, Craig White, and others who have contributed one way or another will forgive me if I concentrate on Gordon this time. I first knew Gordon Grigg long before he first knew me! His reputation extends far and wide as, of course, do his interests. Years before enrolling in an undergraduate science course, I had come across Gordon's work with crocodiles and with kangaroos and I had met some of his former colleagues around the traps. So when I did finally enrol at the University of Queensland and discovered that Gordon had recently become Head of the Zoology Department, I felt lucky and privileged. His lectures on catching crocodiles in the Northern Territory, on tracking echidnas around the southern Alps, on losing fish to seals in the Antarctic were among the highlights of the course. He does not remember me - as a second year student asking permission for something or other - telling him I wanted his job. Or at least, he says he

doesn't! Our first serious conversation came in my third year in the field in western Queensland when we talked about echidnas. I had decided that echidnas were interesting and Gordon supported me, and showed faith in me, through a challenging, though gratifying, honours project involving substantial, remote field work. From there, a PhD. followed (eventually) and I am able to claim that I was his last post-graduate student to submit before he retired. I found Gordon to be generous and supportive in too many ways to mention. As good supervisors should, he took a close interest in my projects, providing advice, equipment and labour when needed. More importantly, he has always taken a close intellectual interest in the work of all those around him, ready to challenge and take colleagues and students off into uncharted territories. To explore with Gordon is so often an attempt to keep up! Nonetheless, the effort is worthwhile and I am privileged to nominate him as a mentor. I hope that subsequent students might find his equal, but I fear that might be a challenge.

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